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INVASION NOTE

Lack of human-assisted dispersal means *Pueraria montana var. lobata* (kudzu vine) could still be eradicated from South Africa

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Abstract The legume, *Pueraria montana* var. *lobata* (kudzu vine) is one of the worst plant invaders globally. Here we present the first study of *P. montana* in South Africa. We found only seven *P. montana* populations covering an estimated condensed area of 74 hectares during the height of the growing season. Based on a species distribution model, it appears that large parts of the globe are suitable, including parts of the eastern escarpment of South Africa (where most populations occur). South African populations of *P. montana* appear to have a similar ecology to populations in the USA: high growth rates, low seed germination, no natural long-distance dispersal, little herbivory and vigorous post-fire resprouting. In contrast to the USA, most South African populations do flower and flowers are capable of producing seed in the absence of pollinators. However, *P. montana* appears to have never been widely planted in South Africa, and the incursion was for many years restricted to a single introduction site. The comparison between the invasions of *P. montana* in the USA and South Africa highlights the often overriding importance of human-assisted dispersal and cultivation in creating widespread invasions, and should serve as a warning to people who have proposed to utilize the species in Africa.

Keywords Africa · Alien invasive weed · Climate models · Fabaceae · Legume · Pollination

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Introduction

One of the best predictors of plant invasiveness is whether a species is invasive elsewhere (see for ex. Herron et al. 2007). Information from one region, in which a species has an established history of invasion, can be used to inform predictions in another region (Pauchard et al. 2004; Diez et al. 2012), and in particular be used to motivate for initiating an eradication attempt (Anderson 2005). Efforts to predict invasiveness can also be based on plant traits (see for ex. van Kleunen et al. 2010), mutualisms (see for ex. Geerts and Pauw 2009), taxonomy (see for ex. Diez et al. 2009) and climate (see for ex. Pheloung et al. 1999). Of these, climate is one of the best predictors, with invasive alien species that have major impacts in one region currently prioritized for control in climatically similar regions where these species start to naturalize (Pauchard et al. 2004; Pheloung et al. 1999). But this begs the question, why is there a substantial difference in observed invasiveness between regions?

Here we explore the case of *Pueraria montana,* one of the world's most damaging invasive species (Forseth and Innis 2004; Friedman 2010). It was introduced to the USA in 1876 and subsequently widely planted as an ornamental, for erosion control, soil stabilisation and as high-nitrogen forage (reviewed in Forseth and Innis 2004). It is a now a widespread invader in the USA, but without data on planting locations it is difficult to assess the importance of direct human dispersal versus natural dispersal, in stimulating these invasions.

Here, for the first time, an invasion of *P. montana* in South Africa is investigated, and we attempt to explain whether the current narrow distribution is due to residence time, climatic conditions, biological factors or some aspect of introduction dynamics. Specifically, we (1) disentangle the introduction history and control of *P. montana* in South Africa, (2) model the worldwide climatic suitability for *P. montana*, (3) map the current and potential distribution in South Africa, and (4) compare the ecology and mechanisms of spread in South Africa and the USA.

Methods

Study species

Pueraria montana (Lour.) Merr. var. *lobata (Willd.) Maesen & S. M. Almeida ex Sanjappa & Predeep* (Fabaceae) is a perennial, climbing vine with deciduous foliage. It grows best in high-light forest-edge areas and can achieve growth rates of 10–30 m per season. Due to its large underground root tubers, plants can rapidly regrow after fires. Flowers are of a typical legume form and borne in compact racemes. The low seed production in the introduced ranges is attributed to a lack of suitable pollinators and insect predation on seeds (reviewed in Forseth and Innis 2004). Natural seed dispersal may be by wind, animals, water and potentially by birds (Burrows 1989), although birds have not been observed and are unlikely (Burrows pers. comm. 2013; pers. obs.). Although vervet monkeys, baboons and guinea fowls were observed at *P. montana* populations in South Africa, no utilisation or seed dispersal by these animals were observed. Despite the range of dispersal vectors, natural seed dispersal distance is generally less than 6 m (Abramovitz 1983; Forseth and Innis 2004). However, long-distance dispersal along corridors such as roads does happen (Pappert et al. 2000).

Introduction history and current distribution in South Africa

A list of all *P. montana* records was compiled from the Southern African Plant Invaders Atlas (SAPIA) (accessed April 2012 (Henderson 1998)), a database of herbarium records (PRECIS 2012), an online spotter network (www.ispot.org.za) and responses to pamphlet distribution to local foresters, conservation officers, botanists and conservationists (Fig. S1). Localities were visited between 2011 and 2014. Current and previous landowners and foresters were interviewed for information on historical control efforts.

All *P. montana* populations were mapped by walking around the perimeter of each clump. We systematically surveyed one population at the start of the growing season, mapped all sprouting rootstocks, and compared this to a map of the patch perimeter obtained later in the season. Based on the quality of the fit between the two methods (Fig. S2), mapping the perimeter of a patch appears to be a reliable measure of sprouting rootstocks and was subsequently used for all other populations. In the area where *P. montana* was first introduced and the most abundant (Barberton, Kaapsehoop and Rosehaugh near Schagen, Nelspruit, Mpumalanga), we did roadside sampling by car of all tarred regional and main gravel roads in the area (excluding those purely in suburbs), for a total distance of 428 km.

Potential *P. montana* distribution in South Africa based on climate

We obtained *P. montana* occurrence records from the Global Biodiversity Information Facility (GBIF 2008; gbif.org/species) and included additional occurrences for South Africa (this study) and Switzerland (Gigon et al. 2014). After data cleaning we were left with 509 occurrences. We used Maxent in the dismo R package to build species distribution models (SDMs) using the aforementioned presence records and 10,000 pseudo-absence records. We selected pseudo-absence records based on the frequency of records of species closely related to *P. montana* (Table S1) within 10' grid cells (Merow et al. 2013). We selected nine environmental variables from the WORLDCLIM dataset as predictors, basing our selection on variables thought to be ecologically important for *P. montana* and also excluding any highly correlated pairs of environmental variables (Table S2; Merow et al. 2013). We ran Maxent and used the randomly selected subset of 70 % of the data for model calibration, and the remaining 30 % for model evaluation using the area under the receiver operating characteristic curve (AUC) and the continuous Boyce Index (Hirzel et al. 2006). We masked areas for which the model is extrapolating into novel environmental space (see supplementary material for detailed methods).

Ecology and mechanisms of spread: pollination, reproduction, seed germination, herbivory and vegetative reproduction

Floral visitors were observed at one site (Rosehaugh population, Sudwala Road; −25.37653°; 30.71592°) and nectar measured (n = 20 flowers) to infer potential pollinators. To establish the ability of *P. montana* to produce fruit autonomously, inflorescences were haphazardly selected and bagged with fine-mesh gauze bags when in bud phase to exclude all visitors (n = 16 plants; 18 inflorescences and 457 flowers). As a control, an adjacent inflorescence was tagged and left open to receive pollinator visits (n = 19 plants; 31 inflorescences and 1268 flowers). Seed viability of naturally produced seeds was tested by germinating them under controlled conditions. Forty haphazardly selected leaves and 78 flowers were examined for herbivore damage. To determine the importance of vegetative reproduction, runner survival was determined under controlled greenhouse conditions. Runners were cut to contain one node, and be 20 cm long and either have no roots (n = 26), contain a few small roots but not rooted in the soil (n = 15) and starting to root in the soil (n = 19). Anecdotal evidence during detailed mapping of all populations, suggests the study population to be representative in herbivory and pollinators (see supplementary material for detailed methods).

Australian weed risk assessment for *P. montana* in South Africa

To assess the potential invasiveness of *P. montana* in South Africa we used the Australian weed risk assessment protocol developed by Pheloung et al. (1999) and the Hawaii Pacific weed risk assessment. This was adapted to South African conditions, by using the predictions of the species distribution model in answering question 2.01 of the protocol (is the species suited to South African climates?).

Statistical analyses

Cutting growth results were analysed with a Chi square test. Generalized linear models with binomial errors were used to compare pods and seeds produced between pollinator-excluded and open inflorescences. Open inflorescences had more (43 %) flowers per inflorescences than bagged branches. We therefore include plant effect and number of flowers as covariates in the analysis. The data on the survivorship of runner fragments were analysed with a Chi square test. All statistical analyses were conducted in R (R Development Core Team 2015).

Results

Introduction history and current distribution in South Africa

Pueraria montana was introduced in the 1920s from Argentina as nutritious fodder for cattle (Chris Dunshea pers. comm., 23rd August 2013) (Fig. 1). It was introduced to one farm only, on which growth and spread was initially limited by heavy grazing. However, the population slowly expanded onto the adjacent riverbank and roadside. Road upgrades (from gravel to tar) during 1975 and 1976, resulted in further spread as road building equipment and forestry trucks inadvertently transported *P. montana* material (Fig. 1; Chris Dunshea pers. comm.). Subsequent spread by roadside mowing equipment has also been reported (Ndlovu 2011). Substantial efforts were made to control *P. montana* during the 1970s and early 1980s, but the project failed (Zimmermann 2011, pers. comm.). From 1982 to 2006, *P. montana* was sporadically and unsuccessfully controlled by local farmers with Triclopyr and grazing by fenced-in goats. Fire as a control method also proved unsuccessful. The first formal record of *Pueraria montana* as invasive in South Africa was only in 1984 (Henderson 1998), with the first published record a few years later (Burrows 1989).

We found seven *P. montana* populations in three provinces covering 74 hectares in total (Table S3; Fig. 2 inset). Most populations occur in the Mpumalanga Province (Fig. 2), with the largest populations in the Schagen district (Rosehaugh) at the initial introduction site (Fig. 2). Currently *P. montana* occurs mostly in forestry plantations (Fig. S3a), road embankments and riparian zones (Fig. S3b), but also in disturbed shrublands and abandoned pastures.

Potential *P. montana* distribution in South Africa based on climate

The SDM model exhibited high predictive accuracy (AUC = 0.91 ± 0.13 95 % CI; continuous Boyce Index = 0.99 ± 0.0002 95 % CI) and predicts *P. montana* occurrence across much of Southeast Asia (the species' native range), Japan, the Koreas, the eastern seaboard of Australia, New Zealand, much of the southeastern USA, southern Brazil, southern Europe and parts of central Africa (Fig. S4). We found that precipitation of the warmest quarter (BIO18) had the largest influence on *P. montana* occurrence, followed by mean diurnal temperature range (BIO2) and temperature seasonality (BIO4) (Table S4). *P. montana* is most likely to occur in regions with high summer rainfall, low diurnal variation in temperature, and intermediate seasonal

Fig. 1 A narrative of *Pueraria montana* history in South Africa highlighting the limited introduction effort and human assisted spread

Year	Narrative
1920s	Introduced from Argentina (for fodder), to one farm in the Rosehaugh district, Mpumalanga
1975-1976	Road building (small gravel track to wide tarred road) spreads *Pueraria montana* along the road
1980s	Government Forestry eradicating Brooklands site, first herbarium record
1980s	Population expand at sites, but no natural spread to new sites. Forestry trucks / road-side mowing spread plants along road-sides
1983+	Sustained control at introduction site (goats, clearing, ineffective herbicide)
1990s	First and only record for Gauteng province (Mamelodi)
2001	First record in KwaZulu-Natal (Pietermaritzburg). In abandoned weed garden of the Cedara Agricultural College
2006	Introduction site sold to SAPPI, threat to forestry recognised and infestations contained
2009	Local farmers set up working group to contain populations
2012	South African National Biodiversity Institute, Invasive Species Programme becomes involved and apply foliar sprays
2013	Management trials and eradication plan developed and implemented

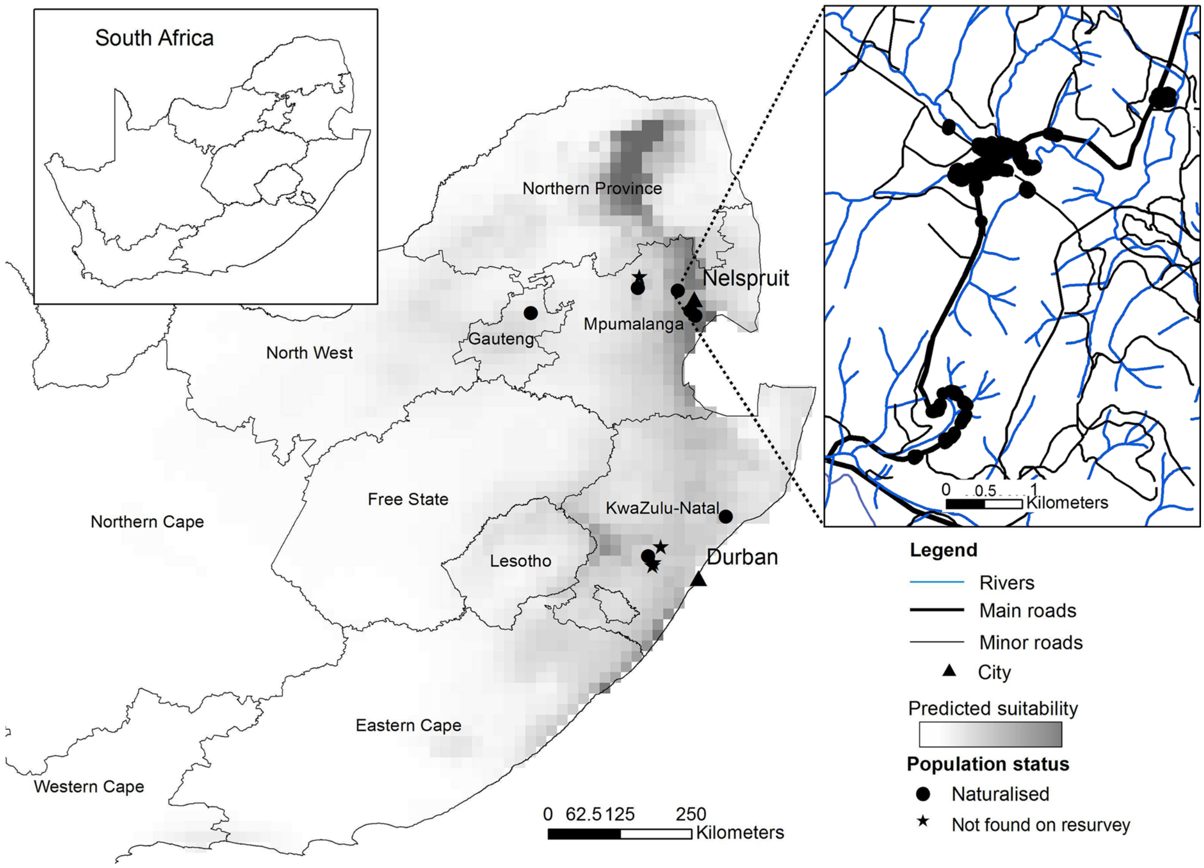

Fig. 2 Distribution of *Pueraria montana* in South Africa. The predicted climatic suitability for *P. montana* is shown (see "Methods" for details), with *darker grey* indicating higher suitability. Inset shows the introduction site at Rosehaugh near Schagen (Nelspruit, Mpumalanga), with subsequent spread along roadsides in all four directions

variation in temperature (Fig. S5). In South Africa climatic suitability for *P. montana* is moderate across much of the eastern escarpment and parts of the KwaZulu-Natal province, with the remainder of the country unsuitable (Fig. 2, Fig. S6).

Ecology and mechanisms of spread: pollination, reproduction, seed germination, herbivory and vegetative reproduction

The typical legume flowers (Fig. S3 c) of *P. montana* are visited by honeybees (*Apis mellifera scutellata*) and carpenter bees (*Xylocopa* spp.). A total of 480 flower-pollinator interactions were observed, with honeybees the most frequent visitors (3.6 visits per flower per hour). This corresponds with the low nectar volume of 0.1 µl (range 0–1.5 µl), and a concentration of 24.5 % (range 23–32 %) sucrose.

Pollinator-excluded inflorescences produced fewer pods (t = 9.4, df = 13, $p < 0.01$; mean in pollinator-excluded 5.3, mean in naturally pollinated 29.7); and fewer seeds per pod (z = 3.5, $p < 0.01$; mean of 2.1 in pollinator-excluded versus 3.6 in naturally pollinated flowers) than control inflorescences.

Only 9 % (4–16 %; 95 % CI) of seeds in the germination trials germinated. This low germination rate is substantiated by the absence of seedlings in the field. No evidence was found that animals consume or disperse seeds. Little leaf damage was observed (Fig. S3 e) with an average of 10 % (range 0–50 %) leaf surface lost due to herbivory by the blister beetle, *Mylabris oculata* (Fig. S3 f). Flowers are damaged at the base (26 % of flowers) by an unidentified leaf-dwelling larva.

After 10 weeks, the survival rate for runners was 4 % for cuttings with no roots, 7 % for those with only a few roots, and 11 % for those with many roots, with no significant difference between the treatments (Chi square test, $\chi^2 = 5.2$, df $= 4$, $p = 0.27$).

Australian weed risk assessment for *P. montana* in South Africa

A score of 26 (Table S5) in the Australian Weed Risk assessment suggests that *P. montana* would fail a pre-border evaluation (Hawaii-Pacific Weed Risk Assessment 2012; Pheloung et al. 1999).

Discussion

Here we argue that *Pueraria montana* is not a widespread invasive plant in South Africa due to a lack of introduction effort, human dissemination and seemingly limited natural dispersal. We show that the global potential distribution of *P. montana* includes many areas of the world. The eastern parts of South Africa are only moderately suitable, with largely similar climatic conditions to the native range, while the remainder of the country has an unsuitable climate. Based on the climatic suitability and invasiveness elsewhere, *P. montana* has the potential to become one of the most serious invaders of the summer rainfall regions in South Africa, including some of the most agriculturally productive and highest conservation value areas of the country (e.g. Kruger National Park). The evidence provided here suggests that there is a barrier to recruitment and that humans are the most important dispersers, which should drive management practices in non-invaded climatically suitable areas of South Africa.

In contrast to the USA, where the enormous increase in area was driven by human introduction and cultivation of seedlings at hundreds of sites (Forseth and Innis 2004), in South Africa there were no concerted efforts to cultivate and spread *P. montana* plants. Where plants are found, they are generally occurring on roadsides, in line with findings from the USA that road building and roadside mowing are important mediators for spread (Kartzinel et al. 2015). However, as survival of runners in this study was low, even this mode of spread is unlikely unless large quantities of plant material are moved around. There are several potential biotic dispersal agents in the region, e.g. primates and birds, but the current distribution is only really consistent with limited natural spread and spread along roads by construction vehicles.

In contrast to the USA, where flowering is rarely observed (Kidd 2002), in South Africa most populations produce flowers, and flowers are frequently visited by native pollinators. Although largely reliant on pollinators for seed production, *P. montana* in South Africa can also produce seeds in the absence of pollinators (4.6 % of pollinator-excluded flowers produced pods in South Africa, while none are produced in the USA). Similarly, only 3.3 % of naturally-pollinated flowers in the USA produced pods (Abramovitz 1983), while 72 % did so in South Africa. Despite this, seed viability in South Africa is low at nine percent, but still within the usual range for non-scarified seeds (Susko et al. 2001). Similar to other Fabaceae species, impermeable seeds of *P. montana* might ensure seed longevity in the soil (Baskin and Baskin 1998; Susko et al. 2001), but no studies have determined the longevity or the size of soil seed banks (Forseth and Innis 2004). With the relative low levels of seed production, the apparent lack of natural dispersal, and the absence of seedlings in the field, seeds seem to currently be of little importance for *P. montana* dispersal in South Africa.

In terms of management, several classical biological control agents have been tested in the USA, but no effective, host-specific agents have been found to date (Frye et al. 2007), and, unless eradication can be ruled out, it does at present not seem to be the most promising option for control in South Africa. Fire can be effective in some circumstances, but it will damage native vegetation, and stimulate *P. montana* resprouting and seed germination (Susko et al. 2001). Therefore, for South Africa we suggest initial control through grazing by goats (Terrill et al. 2003) in riparian populations, whilst focused chemical and mechanical control should attempt to extirpate all other populations. Subsequent physical removal of roots in riparian areas is labour intensive and time consuming, but the only method to ensure eradication. Throughout, close monitoring of current populations is suggested, with emphasis also on searching for new populations. Such a proactive approach against potentially invasive species was until recently rarely undertaken in South Africa (but see Geerts et al. 2013a, b; Wilson et al. 2013), but is recommended for *P. montana*.

This study will serve as an important basis for future work on *P. montana* in South Africa and Africa, which should focus on the following: niche shift and niche conservatism relative to its native range (Callen and Miller 2015); differences in soil chemical properties between South Africa, the USA and the native range; symbiotic relationships with nitrogen-fixing bacteria and the benefit for germination and growth; a genetic analysis to disentangle population relatedness and dispersal sequences in South Africa as these have proven useful to guide management practices (Kartzinel et al. 2015); seed bank size and seed bank longevity; and lastly the influence of the introduction pathway (including molecular analyses), which for South Africa was via Argentina, whilst the USA plants came directly from the native range. These questions should be addressed simultaneously with control, since eradication is critical and should receive priority.

A major concern is that despite the plethora of information on the invasiveness of *P. montana*, there is still a demand for *P. montana*. One such example is a request from tropical Africa for half a tonne of *P. montana* seeds to be grown for fodder (David Orr pers. comm. 2013). This is reason for concern, since plant species are not restricted by country borders, and species introduced in one country are able to spread (aided or unaided) into neighbouring countries. This is particularly concerning in Africa where most countries have limited resources to counter the threat of invasive alien species and little environmental legislation exists or is enforced. More generally, it highlights that impact is largely a function of usage, e.g. biofuel crops and fodder species that are initially dependant on human assistance for establishment and dispersal, but once established could become major invasive species. Potential future examples could include the alien fodder crop, *Cytisus proliferus* (Tree lucerne) advocated as an ideal fodder species for the drier parts of Africa. Closely scrutinising and allowing for monitoring these species via permit systems will go a long way to ensure institutional memory and prevent abandoned plantations or fodder crops from becoming major invaders.

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